Fine-root production and litterfall: main contributions to net primary production in an old-growth evergreen broad-leaved forest in southwestern Japan

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Fineroot production and litterfall: main contributions to net primary production in an old-growth evergreen broad-leaved forest, southwestern Japan

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Abstract

Net primary production (NPP) is an important index for the evaluation of the patterns, processes, and dynamics of carbon cycling in forest ecosystems. In this study, we estimated the NPP in a warm-temperate old-growth evergreen broad-leaved forest in southwestern Japan. The estimation was based on four compartments: aboveground stand increment (ΔM), aboveground litterfall (Lf), fineroot production (Fr), and coarse root increment (ΔCr). The data for ΔM and ΔCr were collected from a permanent 200 × 200 m^2 plot over a 4-year interval and over a 1-year interval for Lf and Fr. NPP was 4.65 g m^{-2} d^{-1}, of which ΔM accounted for 25.2%, Lf accounted for 38.7%, Fr accounted for 33.4%, and the remainder of 2.7% was attributed to ΔCr. There was a significant regression between aboveground litterfall and fineroot production (R^2 = 0.65, P < 0.05). Fineroot decomposition (0.66 g m^{-2} d^{-1}) contributed 14.2% to NPP, leading to higher belowground NPP in the present study as compared to that in other forests. We concluded that to improve accuracy in NPP estimation for forest ecosystems, the estimation of decomposition of dead fineroots by the continuous inflow method must be included.

Keywords: continuous inflow method, decision matrix, fineroot decomposition, litter dynamics, old-growth forest

1. Introduction

Net primary production (NPP) and heterotrophic respiration represent two main fluxes of carbon exchange between the atmosphere and ecosystems. NPP must be considered to understand carbon exchange between the atmosphere and ecosystems (Melillo et al. 1995; Woodward et al. 1995), as NPP is an important index for the evaluation of the patterns, processes, and dynamics of carbon cycling in forest ecosystems at local, regional, and global scales (Luo et al. 2002). The NPP of an ecosystem drives heterotrophic activities and controls net ecosystem production. Because changes in NPP can have global significance and can change ecosystem function and structure (Mooney et al. 1996; Chapin et al. 1998), the quantification of NPP with a reasonable degree of accuracy is required.

Most studies that have estimated NPP of forests considered the increment in aboveground biomass (AGB) and litterfall (Wang et al. 2011; Chambers et al. 2001), and some studies have included the increment of coarse roots (Shvidenko et al. 2008). Recently, several studies included fineroot production in NPP estimation (Ohtsuka et al. 2013; Baishya and Barik 2011; Yashiro 2010), which may contribute up to 50% of total NPP (Vogt et al. 1996). Several methods exist for estimating fine root production (Osawa and Aizawa 2012; Metcalfe et al. 2007; Majdi et al. 2005; Bernier and Robitaille 2004; Hendricks and Pregitzer 1993; Raich and Nadelhoffer 1989; Fairlay and Alexander 1985) and all these methods have advantages and disadvantages. For example, the rhizotron technique (Bernier and Robitaille 2004) used for observing fineroot growth and estimating fineroot production often provides an underestimate because fineroots may branch to several orders at the back of the rhizotron. A decision matrix by Fairley and Alexander (1985), which has been widely used is based on the changes in the mass of both living and dead fineroots during a measurement interval. This estimation underestimates fineroot production because of lack of knowledge about the decomposition of dead fineroots. The continuous inflow method (Osawa and Aizawa 2012) assumes that fineroots grow, die, and decompose

simultaneously. Thus, decomposition of dead fineroots is included in production estimation, leading to a more accurate estimation of fineroot production.

Both the ingrowth core or sequence soil core methods are direct methods that use destructive sampling for estimating fineroot production, and are laborious and technically problematic (Nadelhoffer and Raich 1992). An indirect estimation method may be a viable alternative. Raich and Nadelhoffer (1989) and Davidson et al. (2002) concluded that total annual belowground carbon allocation, which is mostly a contribution of fineroot production (Vogt et al. 1996), is roughly twice that of annual aboveground litterfall carbon.

Evergreen broad-leaved forests are distributed in the warm temperate zone of Japan (Kira 1991). As compared with other forest types in Japan (e.g., deciduous broad-leaved forests in the cool temperate zone), evergreen broad-leaved forests tend to be highly productivity because of warmer climate conditions (Kira 1977). From this perspective, many NPP studies had been conducted in evergreen broad-leaved forests of Japan (Tadaki 1968; Kira and Yabuki 1978; Tadaki 1995; Kubota 2003; Nakagawa et al. 2006; Tada et al. 2006). Although some studies have estimated belowground NPP using the proportion of AGB (Kimura 1960; Kira and Yabuki 1978), NPP data, including belowground values, were limited because of the methodological difficulties experienced. In addition, fineroot growth and loss in evergreen broad-leaved forests remains poorly understood compared with that in other deciduous forest types and coniferous plantations in Japan (Noguchi et al. 2007). Moreover, most studies were conducted in secondary coppice forest. Because natural forest was converted to secondary forest and conifer plantations, or destroyed for other land uses (e.g., settlements and agricultural areas), old-growth evergreen broad-leaved forests remain only within restricted and mountainous areas in Japan (Sasse 1998). The scarcity of NPP data for old-growth forest is one of the limitations preventing the understanding of carbon dynamics in evergreen broad-leaved forest ecosystems. Since 1989, long-term monitoring of stand structure and carbon dynamics has been conducted in an old-growth evergreen broad-leaved forest in southwestern Japan (Tanouchi and Yamamoto 1995;

Sato et al. 1999; Saito 2002; Sato et al. 2010). These monitoring data are beneficial for understanding NPP, including fineroot production in evergreen broad-leaved forest ecosystems.

The aims of the present study are as follows: 1) estimating fineroot production by using the decision matrix and continuous inflow methods and assessing their accuracy and applicability, 2) estimating NPP for a warm-temperate old-growth evergreen broad-leaved forest in southwestern Japan, and 3) searching for an indirect method for estimating fineroot production through regression between fineroot production and aboveground litterfall.

2. Materials and methods

2.1. Site description

The study was conducted in a permanent 200 × 200 m^2 plot (Fig. 1b) established in 1989 for long-term ecological research in a warm-temperate old-growth evergreen broad-leaved forest in southwestern Japan. The plot is located on a steeply inclined north-northwestern slope (32°03′N, 131°12′E), expanding from 380 m to 520 m a.s.l. There are two gullies and a shallow valley without surface water in the plot. More details about the plot can be found in Sato et al. (1999). The plot was used to measure all stems of diameter at breast height (DBH) ≥ 5 cm for estimating AGB and coarse root increments. Since topography considerably affects above and belowground NPP, while we could not collect aboveground litterfall and conduct experiments for estimation of fineroot production in the whole 200 × 200 m^2 plot, sub-plots were used. A subplot (“sub-first”) of 100 × 120 m^2 (Fig. 1b) was established inside the main plot, which included the crest, gully, upper slope, and lower slope. Two litter traps of 42 L volume were set systematically (15 m × 15 m) for aboveground litterfall estimation. Two smaller (“sub-second”) sub-plots of 20 × 20 m^2 each were established inside the sub-first plot for the fineroot experiment: one plot was situated

on the upper slope, facing west and another on the lower slope, facing east.

Average annual rainfall and temperature of the study site is 3,070 mm and 14.2 °C, respectively (Sato et al. 1999). The bedrock of the region consists of Mesozoic shale and sandstone (Kumamoto Regional Forestry Office 1963). A moderately moist Brown Forest soil type predominates. Climate data, including temperature and precipitation during 2013 (Fig. 1a), were collected at a weather station situated approximately 8 km from the study plot, and any extraordinary weather conditions during the study period were excluded; no strong typhoons hit the study site during 2012 and 2014, when this study was conducted. There is no dry season at the study site. Minimum monthly precipitation is 72 mm during December, while the maximum during June is 467 mm. All months have > 11 rainy days. There are six months of winter (November–April) with minimum temperature dropping to 3 °C during January, and six months of summer with maximum temperatures rising up to 32 °C during July–August.

Vegetation in the study site is known as old-growth forest, as there are no signs of human disturbances, such as logged stumps and burning (Sato et al. 1999). The forest is dominated by evergreen trees including *Distylium racemosum, Persea thunbergii*, *Quercus acuta*, *Quercus salicina*, and *Quercus gilva*. In addition, there are a few deciduous broad-leaved species such as *Cornus controversa* and *Carpinus tschonoskii*. A total of 36 evergreen broad-leaved species and 13 deciduous species were identified in a 4-ha plot with a total of 4,668 individuals of DBH ≥ 5 cm and a basal area of 217 m^2 (Sato et al. 1999).

2.2. NPP estimation

There are four compartments included in NPP estimation as shown in Equation 1:

$$\mathrm{NPP} = \Delta\mathrm{M} + \Delta\mathrm{Cr} + \mathrm{Lf} + \mathrm{Fr}, \quad (1)$$

where ΔM is aboveground stand increment, ΔCr is coarse root increment, Lf is aboveground litterfall, and Fr is fineroot production. The herbivore loss by insects and wildlife is assumed to be negligible.

2.2.1. Aboveground stand increment

ΔM was estimated in the manner described below. DBH of all ≥ 5 cm living stems was measured during November 2009 and November 2013 and recorded separately for four 1-ha plots in a permanent 4-ha plot (Fig. 1b) to estimate ΔM over the 4-year period. Aboveground stand increment of each 1-ha plot was estimated as shown in Equation 2 (Clark et al. 2001):

$$\Delta M = \sum_{\text{stem } 1}^{\text{stem n}}(\text{AGB}_{\text{stem i}_{\text{in 2013}}} - \text{AGB}_{\text{stem i}_{\text{in 2009}}}) + \sum_{\text{stem } 1}^{\text{stem j}}(\text{AGB}_{\text{ingrowth stem j}_{\text{in 2013}}} - \text{AGB}_{\text{ingrowth stem j}_{\text{at DBH=5 cm}}}). \quad (2)$$

AGB (kg dry weight) of each stem was calculated as the sum of leaf biomass (W_f) in Equation 3 and biomass of stems and branches (W_c) in Equation 4:

$$\log(W_f) = 1.89\log(DBH) - 1.58, \quad (3)$$

$$\log(W_c) = 2.34\log(DBH) - 0.87, \quad (4)$$

where DBH is the diameter at breast height in cm. Equation 3 and 4 were established based on destructive sampling in the old-growth forest, close to the present study site (Kimura 1960). The

mean of the differences of standing biomass between 2013 and 2009 of four 1-ha plots was used as ΔM.

2.2.2. Coarse root increment

ΔCr was estimated based on the relationship between coarse root biomass (CRB) and AGB (Mokany et al. 2006) in Equation 5:

$$\mathrm{CRB} = 0.489\mathrm{AGB}^{0.890}. \quad (5)$$

CRB was separately estimated for each 1-ha plot based on its AGB. The mean of the CRB differences between 2009 and 2013 of four 1-ha plots was then used as ΔCr. Equation 5 was established based on data from forests worldwide.

2.2.3. Aboveground litterfall

Lf (including all falling materials as leaves, branches, and productive organs) was estimated based on 42 litter traps of 0.58 m^2 each, distributed systematically (15 m × 15 m) in 1.2-ha core plot in a permanent 4-ha plot (Fig 1b), of which two traps were disturbed and were therefore excluded in the data analysis. Generally, litter was collected from litter traps over one month intervals (collected on 11 occasions between January 6, 2013 and January 3, 2014). The litter was then oven-dried at 105 °C to a constant mass and weighed for dry mass.

2.2.4. Fineroot production

Fr (fineroot production) was estimated based on the continuous inflow method (Osawa and Aizawa 2012) in Equation 6:

$$Fr = \left(B_j - B_i\right) + \left(N_j - N_i\right) + \left[-\left(N_j - N_i\right) - \left(\left(N_j - N_i\right)/\gamma_{ij} + N_i\right) * \ln\left(1 - \gamma_{ij}\right)\right], \quad (6)$$

where B_i and B_j are the masses of living fineroots (biomass) at time t_i and t_j, respectively ($t > t_i$); N_i and N_j are the masses of dead fineroots (necromass) at time t_i and t_j, respectively; and γ_{ij} is the decomposition ratio of dead fineroots between t_i and t_j. Sequential soil core sampling was used

for B_i, B_j, N_i, and N_j, whereas the litter bag technique was used for γ_{ij}.

For sequential soil core sampling, a stainless steel tube of 36 mm in diameter (inner diameter of 34 mm) was used to sequentially core the ground to the depth of 21 cm four times; on 7 January, 14 May, November 25, 2013, and January 9, 2014. On each sampling date, 40 soil cores (20 soil cores for each plot) were collected systematically with a spacing of 2 m × 4 m from two subplots of 20 × 20 m^2 (Fig. 1b). Fineroots were separated from the collected cores by washing and sieving. The fineroots were then classified into dead and live roots. The live and dead fineroots were differentiated by their color, resilience, and structural integrity (Hishi and Takeda 2005). Roots were then dried in a forced-air oven at 70 °C until constant mass, and the mass of live roots and dead roots was weighted separately.

The litter bag technique was used for γ_{ij}. Envelope-type root litter bags composed of special cloth (root-impermeable water-permeable sheet/RIWP, Toyobo Co., Osaka, Japan) were used. The RIWP has a pore size of approximately 0.6 μm, which practically blocks ingrowth of fineroots; however, fine soil particles, water, and microorganisms could penetrate through the sheet. Dead fineroots were collected from the field, washed free of soil, and then oven-dried at 70 °C until constant mass. Oven-dried fineroots totaling 1 g was placed into an envelope-type root litter bag (10 cm × 10 cm). Litter bags were systematically buried at a soil depth of 10–15 cm in a spacing of 2 m × 4 m in two 20 × 20 m^2 subplots (Fig. 1b). On January 7, 2013, 30 litter bags (15 bags for each subplot) were buried in the field. On May 14, 2013, 10 litter bags were collected and 20 new litter bags were buried in the field. On November 25, 2013, the ten litter bags buried on January 7, 2013 and May 14, 2013, respectively, were collected, and 10 new litter bags were buried. On January 9, 2014, the 10 litter bags buried on January 7, 2013, May 14, 2013, and November 25, 2013, respectively, were collected. Collected litter bags were washed, and then oven-dried for remaining mass, which was used to estimate γ_{ij} [γ_{ij} = (initial mass − remained mass)/initial mass] for corresponding time intervals (Osawa and Aizawa 2012).

Fineroot decomposition, mortality, and production were also estimated by the decision matrix (Fairley and Alexander 1985) to compare with those determined using the continuous inflow method. The decision matrix was based on ΔN (N_j-N_i) and ΔB (B_j-B_i) without knowledge of γ_{ij}: ***(1)*** if $\Delta B \geq 0$ and $\Delta N \geq 0$, g_{ij} (fineroot production) = $\Delta B + \Delta N$, m (mortality) = ΔN, d (composition = 0); ***(2)*** if $\Delta B \geq 0$ and $\Delta N < 0$, $g_{ij} = \Delta B$, m = 0, d = $-\Delta N$; ***(3)*** if $\Delta B < 0$, $\Delta N > |\Delta B|$, and $\Delta N \geq 0$, $g_{ij} = \Delta B + \Delta N$, m = ΔN, d = 0; ***(4)*** if $\Delta B < 0$, $\Delta N > |\Delta B$, d co$\Delta N < 0$, g_{ij} = 0, m = $-\Delta B$, d = $-\Delta B - \Delta N$; ***(5)*** if $\Delta B < 0$, $\Delta B > |\Delta N|$, and $\Delta N \geq 0$, $g_{ij} = 0$, m = $-\Delta B$, d = $-\Delta B - \Delta N$; and ***(6)*** $\Delta B < 0$, $\Delta B > |\Delta N$, and o$\Delta N < 0$, $g_{ij} = 0$, m = $-\Delta B$, d = $-\Delta B - \Delta N$.

2.3. Statistical analysis

Spatial variation in ΔM and ΔCr was quantified as standard errors. First, 200 × 200 m^2 plots were divided into four 1-ha plots. Aboveground biomass during 2009 and 2013 was estimated for the four 1-ha plots individually. The difference of biomass between 2009 and 2013 (a 4-year basis) was then calculated for the four 1-ha plots individually. The mean of the biomass difference and the standard error from the four 1-ha plots is represented as ΔM and its standard error. The yearly basis of ΔM was then calculated by dividing the 4-year basis by four. The same process was applied to ΔCr and its standard error. The spatial variation of Lf was quantified as the standard error and was estimated in the following manner: in each collection, the mean of Lf from 40 undisturbed traps and its standard error represented values of that month. The mean and standard error from 40 undisturbed traps of aboveground litterfall in all 11 collections were the annual mean and its standard error.

For the estimation of fineroot production, 40 cores collected on each date were randomly divided into 10 groups of four cores each. The means of the four cores were used to estimate production, mortality, and decomposition by either the decision matrix or the continuous inflow

method, resulting in output of 10 values. The mean and its standard error of these 10 values represented means of production, mortality, and decomposition with their standard errors. The comparison of fineroot production, mortality, and decomposition between the decision matrix and the continuous inflow method and between the upper slope plot and the lower slope plot was conducted with a *t*-test, which does not assume equal variances. The differences of biomass, necromass, decomposition ratio, production, mortality, and decomposition among the three collected intervals (January 7–May 14, May 15–November 25, and November 26–January 9) estimated by the continuous inflow method were assessed by the univariate analysis of variance (ANOVA) and the post-hoc Tukey's test.

Regressions between fineroot production and aboveground litterfall were conducted based on best fitted model, as indicated by the lowest *P* (probability) and highest R^2 (regression square).

3. Results

3.1. Fineroot production

Fineroot biomass (mass of living fineroots) was significantly greater (*t*-test, $P < 0.05$) than necromass (mass of dead fineroots) over all four collection dates (Fig. 2a). In addition, values of necromass and biomass were dependent on the time of collection (ANOVA: $F_{3,156} = 33.8$, $P < 0.01$; post-hoc Tukey's test: $P < 0.01$), which were highest on January 9, 2014, followed by November 25, May 14, and January 7, 2013. The decomposition ratio of dead fineroots was significantly different (ANOVA: $F_{2,54} = 10.6$, $P < 0.01$; post-hoc Tukey's test: $P < 0.01$) among the three periods. It was highest during summer (May 15–November 25) and lowest during winter

(Fig. 2b).

Fineroot decomposition, mortality, and production were significantly higher (*t*-test, $P < 0.05$) in the continuous inflow method than in the decision matrix method because decomposition was included in the estimation (Fig. 3). Fineroot decomposition, mortality, and production were significantly different (ANOVA: values of $F_{2,27} > 35$, $P < 0.001$; post-hoc Tukey's test: $P < 0.001$) between collected intervals (Fig. 4) and were highest during May 15 –November 25 (0.81, 1.3, and 1.91 g m^{-2} d^{-1}, respectively) and was lowest during November 25–January 9 (0.45, 0.64, and 0.90 g m^{-2} d^{-1}, respectively) (Fig. 4). Meanwhile, there was no significant difference (*t*-test, $P > 0.05$) in fineroot production, mortality, and decomposition (Fig. 5) between the upper and lower slope plots (Fig. 1b). Total fineroot production was 1.55 g m^{-2} d^{-1}, equivalent to 5.66 Mg ha^{-1} y^{-1} (Table 1).

3.2. Aboveground litterfall

Aboveground litterfall (Fig. 6) was highest during April (4.3 g m^{-2} d^{-1}; of which leaf mass was 2.57 g, branch mass was 1.06 g, and productive organ mass was 0.13 g), followed by May (4.0 g m^{-2} d^{-1}; of which leaf mass was 3.36 g, branch mass was 0.05 g, and productive organ mass was 0.07 g). The lowest value was evident during February (0.3 g m^{-2} d^{-1}; of which, leaf mass was 0.20 g, branch mass was 0.04 g, and productive organ mass was 0.003 g) followed by January (0.4 g m^{-2} d^{-1}; of which leaf mass was 0.20 g, branch mass was 0.16 g, and productive organ mass was 0.003 g) and December (0.7 g m^{-2} d^{-1}; of which leaf mass was 0.48 g, branch mass was 0.19 g, and productive organ mass was 0.001 g). Total aboveground litterfall was 1.80 g m^{-2} d^{-1}, equivalent to 6.57 Mg ha^{-1} y^{-1} (Table 1).

3.3. AGB and coarse root increments

Stems with 5 cm ≤ DBH < 15 cm accounted for only 7.3% AGB (Fig. 7a) but 18.5% aboveground stand increment (ΔM, Fig. 7b). Whereas, stems with 55 cm ≤ DBH < 65 cm contributed to the highest AGB (13.5%) but only 10.9% ΔM. In general, 5 cm ≤ DBH < 55 cm stems accounted for 44.9% AGB and 62.4% ΔM. Total ΔM was 1.17 g m^{-2} d^{-1}, equivalent to 4.27 Mg ha^{-1} y^{-1}. Whereas total coarse root increment was 0.13 g m^{-2} y^{-d}, equivalent to 0.46 Mg ha^{-1} y^{-1} (Table 1).

3.4. Total NPP and regression analysis

The total NPP was 16.96 Mg ha^{-1} y^{-1} (Table 1), in which aboveground litterfall accounted for the highest percentage of 38.7%, following fineroot production of 33.4%, aboveground stand increment of 25.2%, and coarse root increment of only 2.7% of total NPP.

Positive linear was well fitted for regression between fineroot production and total aboveground litterfall (R^2 = 0.65, P < 0.05; Table 2).

4. Discussion

4.1. The importance of including decomposition in fineroot production estimation

In the present study, we clarified the importance of including decomposition in the estimation of fineroot production. The fineroot production estimated by the decision matrix was 0.82 g m^{-2} d^{-1}, whereas it was 1.55 g m^{-2} d^{-1} by the continuous inflow method (Fig. 3). The continuous inflow method included decomposition of dead fineroots in the estimation of production as compared with the decision matrix, which ignored this process (Fig. 3), leading to an underestimation of belowground NPP (BNPP) by 89%. Fineroot decomposition (0.66 g m^{-2} d^{-1}) contributed 42.6% of total fineroot production (Fig. 3) and 14.2% total NPP in the present

study. In contrast, decomposition was estimated as zero in the decision matrix (Fig. 3) because of lack of knowledge about the decomposition ratio (Fairley and Alexander 1985). Using scanned images of fineroots, Dannoura et al. (2008) showed that fineroots grow, die, and decompose continuously. Therefore, the setting of decomposition as zero in the decision matrix from only knowledge of changes in the mass of living and dead fineroots obviously leads to an underestimation of fineroot production.

Osawa and Aizawa (2012) first applied the continuous inflow method to a *Chamaecyparis obtuse* plantation. In the present study, the method was extended to a warm-temperate old-growth evergreen broad-leaved forest. We found that there is no restriction for applying the continuous inflow method. A concerning and important point to consider when applying this method is how we can identify the initial mass of dead fineroots in litter bags for a more accurate estimation of the decomposition ratio. Osawa and Aizawa (2012) used air-dried dead fineroots for the estimation of initial mass to reduce the differences of dead fineroots inside litter bags and those in nature. However, this method may result in error from identifying moisture content of air-dried dead fineroots, whereas dead fineroots in litter bags after collecting were oven-dried for the remaining mass. To reduce such error, in the present study, both initial and remaining mass of fineroots were oven-dried. In the present study, before burying in the field, litter bags were immersed in water for 24 h to ensure that the fineroots inside the litter bags were water-saturated, as they would be in nature, for an equal chance of being decomposed.

4.2. NPP in the present study site

Most previous studies ignored decomposition in estimating fineroot production (Table 3) because of applying different estimation methods. For the methods based on relationships between the DBH and root biomass (Tadaki 1968) and fineroot biomass and basal area (Yashiro et al. 2010), it was impossible to collect all fineroots from the destructive sampling of individual

trees for allometry establishment; fineroots have short longevity and a high turnover rate (Vogt et al. 1996), leading to an underestimate. The approach of summing up the positive increments in live root biomass and concurrent positive increment in the dead fineroot biomass (Baishya and Barik 2010), as well as summing up all fineroot mass ingrown to ingrowth cores (Tateno et al. 2004; Girardin et al. 2010), ignored decomposition of dead fineroots (Table 3). This would be the reason why estimated BNPP was highest in the present study site. Aboveground estimated NPP (ANPP) in the present study site is lower than that in the tropical rain forests in Pasoh (6.41 g m^{-2} d^{-1}) and Borneo (5.41 g m^{-2} d^{-1}) in Malaysia and in an old-growth *Pinus kesiya* forest (4.41 g m^{-2} d^{-1}) in northeastern India because of higher radiation and species diversity at these sites (Kitayama and Aiba 2002). However, the ANPP in the present study site is much higher than that in certain other forests (Table 3). Even though the present site is known as an old-growth forest, the site was hit by a strong typhoon during 1993 (Sato et al. 2010), leading to numerous small-sized stems, which were characterized by high ANPP (Fig. 7). A 14-year-old *Castanopsis cuspidata* stand situated close to the present study site had higher total NPP (6.22 g m^{-2} d^{-1}) than that in present study (4.65 g m^{-2} d^{-1}), giving an indication of the effects of stand age on total NPP. In conclusion, total NPP is affected by the estimation methodology and other factors including forest type, climate conditions, and the ages of forest stands.

It is believed that fineroot production is affected by topography (Vogt et al. 1996) from differences including edaphic and tree stem density. However, fineroot production (Fig. 5) between the upper and lower slope plot in the present study (Fig. 1b) was not significantly different because there were no differences of edaphic condition (Ohnuki 1998) and vegetation (Sato et al. 1999) between the two plots. Spatial variation of the aboveground litterfall among the litter traps over all collected dates was small, indicating the representative aboveground litterfall experiment. These confirmed the certainty of total NPP estimation for a warm-temperate old-growth evergreen broad-leaved forest in southwestern Japan.

Generally, small-sized stems are young stems, which are more numerous than bigger-sized stems in the present study site. Therefore, the small-sized stems had higher ΔM (Fig. 7). This is consistent with a conclusion that young and middle-aged forest stands have higher NPP than old-growth stands (Chen et al. 2002; Wang et al. 2011). Stems with DBH ≥ 95 cm accounted for 8.1% AGB but only 6.5% NPP (Fig. 7). It appears that any natural disturbances such as typhoons (Sato et al. 1999, 2010) will not reduce NPP in the present study site, even when large-sized stems fall down, because gaps are soon replaced by numerous small-sized stems. Slik et al. (2013) indicated that increasing temperature due to climate change will significantly reduce the density of DBH > 70 cm stems and their AGB for lowland forests, such as in the present study site. This again may not affect NPP in the present study site. However, it will affect the net ecosystem production, as increasing temperature leads to higher decomposition of dead material in forests (Schimel et al. 1994; Aiba and Kitayama 1999).

4.3. Relationships between fineroot production and litterfall

Positive linear was well fitted for regression between fineroot production and total aboveground litterfall ($R^2 = 0.65$, $P < 0.05$). Fineroots function to absorb water and nutrients to sustain the life of trees. In contrast, evergreen broad-leaved species mainly shed old leaves during the development of new leaves (Nitta and Ohsawa 1997), which occurs during April and May, i.e., early summer in the present study site (Tanouchi and Yamamoto 1995). Therefore, accelerating fineroot production is required to sustain leafing. This suggests that aboveground litterfall may be an alternative indirect method for estimating fineroot production. Further data collection is required for regression confirmation.

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Table 1 Contribution of each compartment to total net primary production (NPP).

	Belowground NPP		Aboveground NPP		Total
	Coarse root increment (∆Cr)	Fineroot production (Fr)	Aboveground litterfall (Lf)	Aboveground stand increment (∆M)	
Mg ha^{-1} y^{-1}	0.46 ± 0.04	5.66 ± 2.15	6.57 ±0.32	4.27 ± 0.40	16.96
Ratio (%)	2.7	33.4	38.7	25.2	100

Table 2 Relationships of aboveground litterfall with fineroot decomposition, mortality, and production.

	Fineroots (g m^{-2} d^{-1})		
	Decomposition	Mortality	Production
Aboveground litterfall (g m^{-2} d^{-1})	$y = 0.24\,x + 0.14$ $R^2 = 0.46$ $P > 0.1$	$y = 0.48\,x + 0.03$ $R^2 = 0.61$ $P > 0.1$	$y = 0.76\,x - 0.07$ $R^2 = 0.65$ $P < 0.05$

In above equations, x is aboveground litterfall and y is decomposition, mortality, or production.

Table 3 Aboveground net primary production (ANPP) and belowground net primary production (BNPP) of different forest types around the world.

Forest type	Study location	ANPP ($g\ m^{-2}\ d^{-1}$)	BNPP ($g\ m^{-2}\ d^{-1}$)	Sources
A warm-temperate old-growth evergreen broad-leaved forest, southwestern Japan	32°03' N, 131°12' E	2.97	1.68*	The present study
Tropical rain forests on Mount Kinabalu, Borneo, Malaysia	6°5'N, 116°33'E	5.41	Not available	Kitayama and Aiba 2002
A 14-year-old *Castanopsis cuspidata* stand	Kumamoto, Japan (close to the present study site)	4.81	1.41*, a	Tadaki 1968
An old-growth *Pinus kesiya* forest, northeastern India	25°55'N, 91°88'E	4.41	0.38*, b	Baishya and Barik 2011
Tropical forest in the Peruvian Andes	13°11'S, 71°35'W	3.72	1.48*, c	Girardin et al. 2010
Tropical forest in central Amazon	2°30'S, 60°W	3.53	Not available	Chambers et al. 2001
A cool-temperate broad-leaved deciduous forest, central Japan	35°18'N, 135°43'E	1.92	1.15*, c	Tateno et al. 2004
An old-growth *Cryptomeria japonica* plantation, central Japan	36°08'N, 137°22'E	1.59	0.56*, d	Yashiro et al. 2010
Tropical forest in the Peruvian Andes	12°49'S, 69°16'W	0.99	0.41*, c	Girardin et al. 2010
An old-growth *Larix gmelinii* stand, central Siberia	64°19'N, 100°13'E	0.49	Not available	Kajimoto et al. 1999

In column BNPP, asterisk indicates including fineroot production. [a] The relationship between root biomass and diameter at breast height of individual tree was used for BNPP estimation. [b] The annual root production was measured by summing up the positive increments in live root biomass and concurrent positive increment in the dead root biomass during the successive samplings (decision matrix). [c] Using ingrowth core technique and summing up all fineroot mass ingrown to cores. [d] Basing on relationship between fineroot biomass and basal area, and fineroot turnover rate of 0.69%.

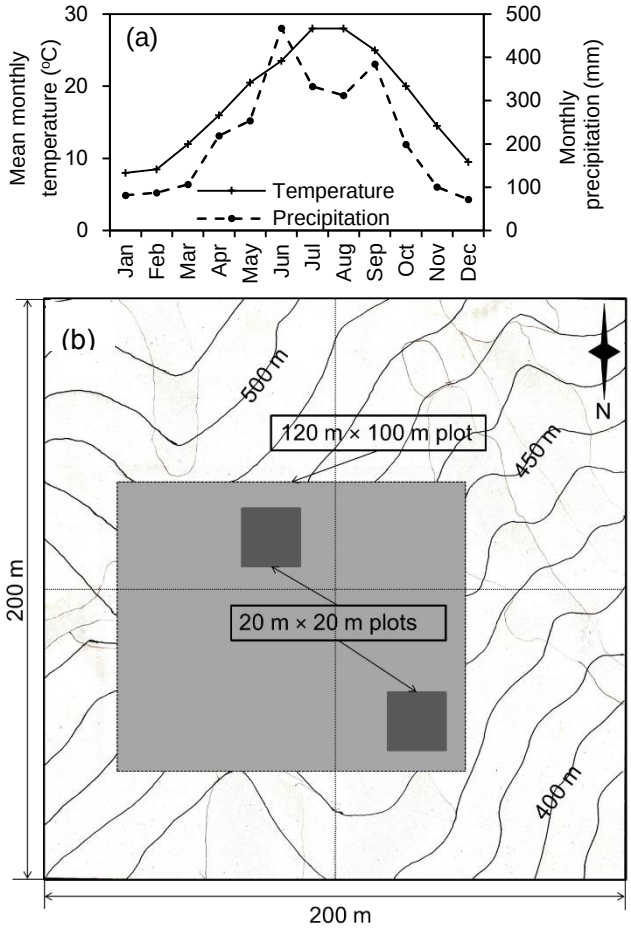

Fig. 1 Temperature and precipitation of the study site during 2013 (a) and the experimental layout of 4-ha plot (b). In (b), a 200 m × 200 m plot was used for the DBH ≥ 5 cm stem census, the 100 m × 120 m plot (medium shaded area) was used for setting 42 litter traps for monthly aboveground litterfall collection, and the 20 m × 20 m plots (heavily shaded areas) were used for the fineroot experiment

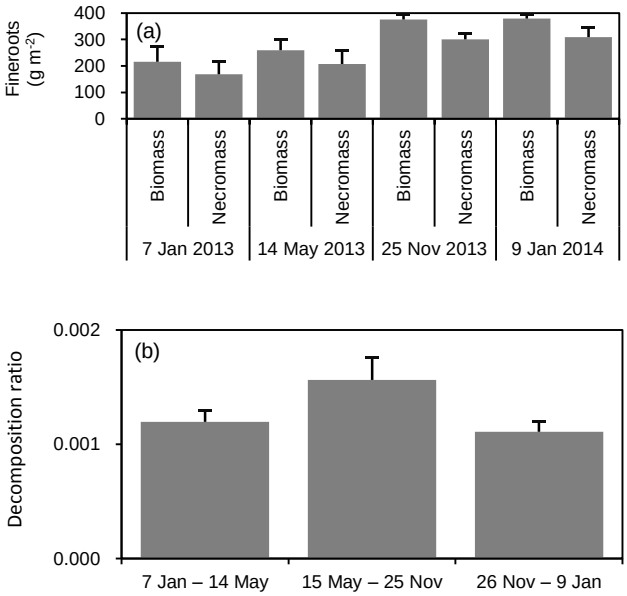

Fig. 2 Mass of live fineroots (biomass) and dead fineroots (necromass) at each collected date (a) and decomposition ratio (dimensionless, ratio d^{-1}) for each collected interval (b). Bars indicate mean + standard error

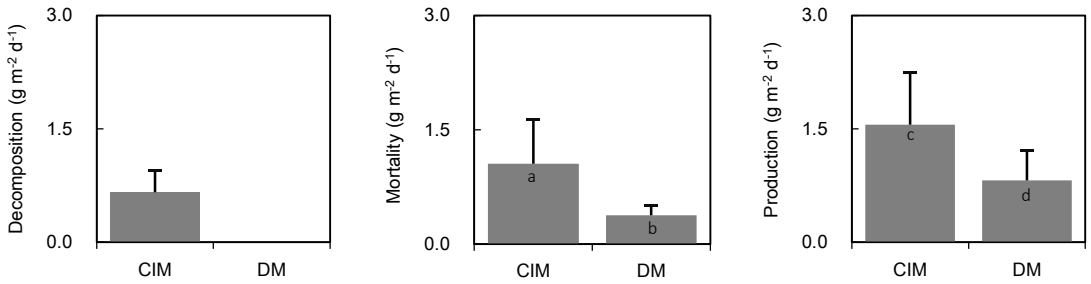

Fig. 3 Fineroot decomposition, mortality, and production estimated by the continuous inflow method (CIM) and the decision matrix (DM). Different letters in bars indicate the difference in mortality and production between the two methods by the *t*-test ($P < 0.05$). Bars indicate mean + standard error

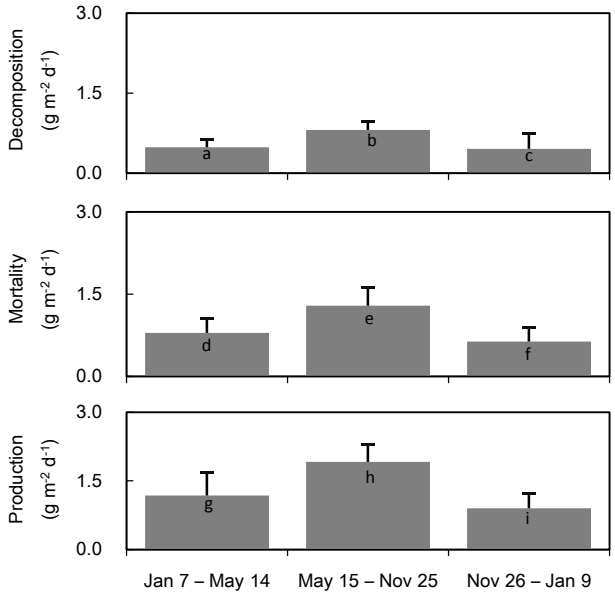

Fig. 4 Fineroot decomposition, mortality, and production for three collection intervals estimated by the continuous inflow method. Different letters in bars indicate the difference of decomposition, mortality, and production between collected intervals by univariate analysis of variance (ANOVA) and the post-hoc Tukey's test. Bars indicate mean + standard error

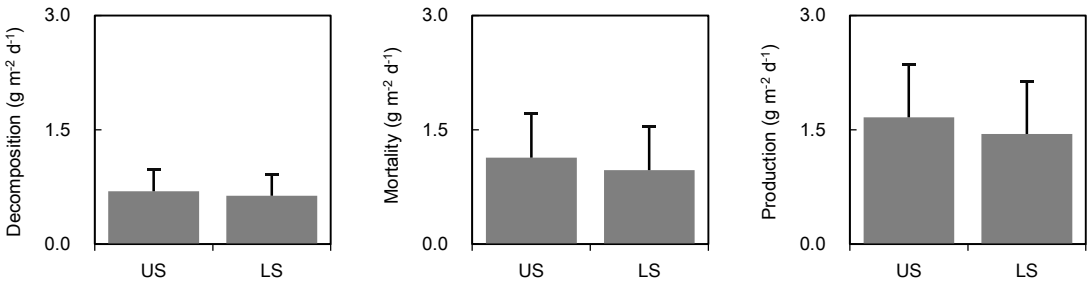

Fig. 5 Fineroot decomposition, mortality, and production in the upper slope (US) and the lower slope (LS) plots estimated by the continuous inflow method. Bars indicate mean + standard error

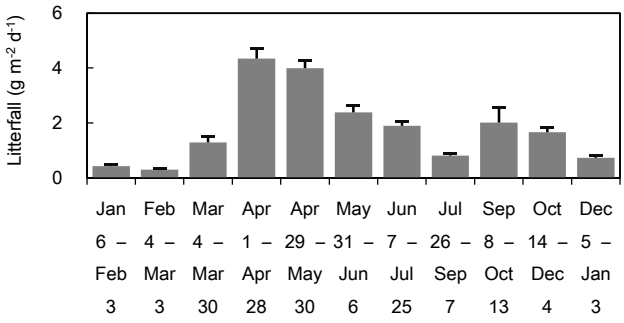

Fig. 6 Dry aboveground litterfall by collected intervals.

Bars indicate mean + standard error

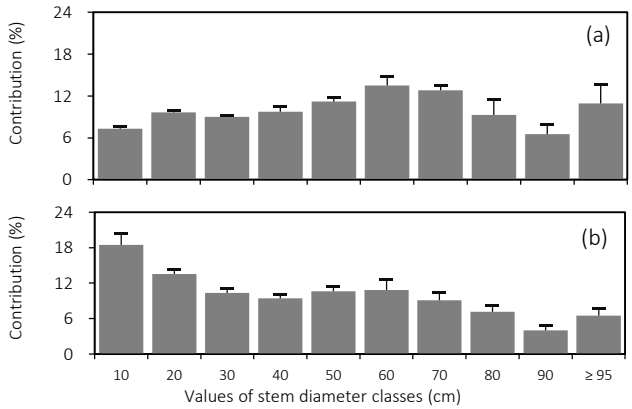

Fig. 7 Contribution of diameter classes to aboveground biomass (a) and aboveground stand increment (b). Bars indicate mean + standard error. Diameter classes of 10 cm were used